



Polinización

Beneficios

- **Planta:** Reproducción (semillas)
- **Animal:** Alimento (nectar y polen, aceite y semillas)
Refugio
Sitios de apareamiento
Materiales de construcción (resina)
Hornos solares







Polinizadores animales:

Abejas, Mariposas, Pollilas, Dipteros, Picaflores,
hormigas, roedores, aves, lemures, primates.

¿Mutualismo?

Punto de vista de la planta:

- Contacte anteras y estigma
- Deposite altas cargas de polen por visita
- Disperse polen de un determinado donante a muchas plantas receptoras
- Visite pocas flores por planta y se mueva frecuentemente entre plantas

Punto de vista del polinizador:

- Obtener la mayor cantidad de energía con un mínimo de movimiento



Yucca Moth

Keeping a critical appointment with their host plant, yucca moths emerge to mate (top, far left) just as pollen-laden yucca flowers unfold. Mating done, the female climbs atop one of the flower's six stamens (top center) and gathers a cache of pollen, using tentacles tailor-made for the task. Airlifting the cargo to another yucca, she bores into the plant's ovary with the ovipositor on her abdomen (top right) to place an egg inside. She then ascends to the stigma and stuffs some pollen into the funnel (left) to fertilize seeds that grow to become food for her larval offspring.

"It's as if the moths are farming the plants," observes biologist and Sociologist Olle Pellmyr. Such gardening pays obvious dividends for the moths, but what for the plants? Pellmyr's cost/benefit analysis shows that the moths' fail-safe pollination service is worth the price of a few seeds.

DARLYNE MURAWSKI reports



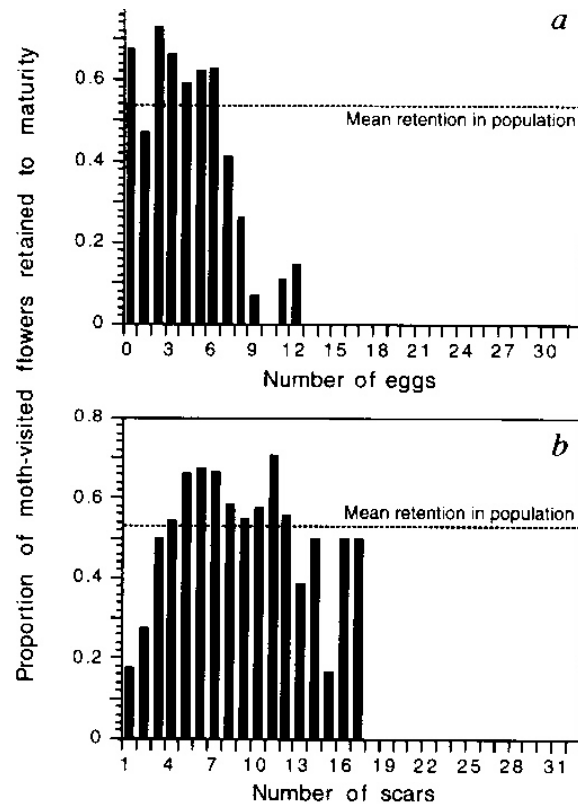


FIG. 1 Proportion of retained flowers for each *Tegeticula* egg and scar number category. Dashed lines indicate grand mean retention in the entire sample. Flowers were tagged on their opening day with a $1 \times 3 \text{ mm}^2$ label giving plant identity and date. Abscised flowers were collected each morning throughout the flowering period and fruit maturation, and ripe fruits were harvested just before dehiscence. During dissection, the number of moth eggs (exit holes for ripe fruit) and total number of oviposition scars were recorded. 10.5% of the labelled flowers were excluded because degradation was too extensive to allow safe counts. For the present analysis, all flowers attacked by the nitidulid beetle *Carpophilus melanopterus* were removed. Larvae and adults of this beetle attack all stages from buds to young fruit and invariably cause abscission. Thus the cause of abortion could not be determined in these flowers. A total of 559 moth-visited flowers were used in the analyses. Flowers with high egg and scar numbers were pooled to meet sample-size requirements for statistical analysis: in a, 15–17 eggs, 18–20 and >20 eggs were combined as cohorts; in b, 10–11 scars, 12–14, 15–17 and >17 scars were combined. Sample sizes by category for the eggs (0–28) were: 49, 64, 85, 68, 68, 58, 48, 39, 23, 14, 8, 9, 7, 3, 5, 1, 4, 1, 2, 1, 1, 0, 0, 0, 0, 0, 0, 0, 1, and for the scars (1–32): 40, 29, 32, 59, 68, 64, 60, 55, 40, 26, 27, 18, 13, 6, 6, 2, 4, 4, 1, 2, 1, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1.

Pellmyr, O. y C.J. Huth.
1994. Evolutionary
stability of mutualism
between yuccas and yucca
moths. *Nature* 372: 257-
260.



Early cheaters

Y. filamentosa - TN

Y. filamentosa - OH

Y. glauca - KS

Y. intermedia - NM

100

FIG. 1 Phylogenetic relationships among pollinating and cheating yucca moths as estimated from a 2.1-kb mitochondrial DNA sequence. *Greya* and *Mesepiola* were chosen as outgroups based on morphological and molecular data²⁷. All *Tegeticula* species are labelled by *Yucca* host and US state. Members of the *T. yuccasella* complex were selected as pairs of coexisting pollinators and cheaters for each taxon; for *Yucca glauca*, two pollinators were included because they coexisted with different cheater taxa. For *Y. baccata* and *Y. utahensis*, known 'late cheaters' were not available for DNA analysis. Hosts of the *T. yuccasella* complex are either capsular-fruited or fleshy-fruited, with *Y. baccata*, *Y. schidigera* and *Y. torreyi* being members of the monophyletic fleshy-fruited species²⁸. Most entities on different hosts are readily diagnosable based on morphological and biological differences (O.P. and J.L.-M., manuscript in preparation). Sequence divergence²⁰ within the complex was 0.7–4.0%. The data were analysed by applying the maximum-parsimony (MP) criterion²⁹ in a heuristic search with random addition (25 replicates). The topology shown is a strict consensus of the two most parsimonious trees yielded, 761 steps in length, with a consistency index of 0.75; the MP trees differed only in how the sole polytomy was resolved. Maximum-likelihood (ML) analysis assuming a Kimura 2-parameter model of evolution with a transition–transversion ratio of 2 yielded one of the two MP trees. Numbers at the nodes give percentage bootstrap support from 500 replicates using the heuristic algorithm. Pollinator function was mapped as an irreversible character, that is, that pollination would re-evolve once lost was considered impossible.

METHODS. A 2.1-kb mtDNA fragment corresponding to positions 1495–3603 in the *Drosophila yakuba* mtDNA genome³⁰ (across the COI–COII and the intervening tRNA_{leu}) was amplified by the polymerase chain reaction (PCR) and both strands were directly sequenced. No insertions or deletions were observed, therefore alignment was readily done by eye, yielding 2,103 sites, of which 519 were variable, and 232 were phylogenetically informative. PCR primer sequences and complete sample data are available from the authors. Moth vouchers will be placed in the Smithsonian Institution (USNM). All DNA sequences have been placed in GenBank under accession numbers U49021–U49043.

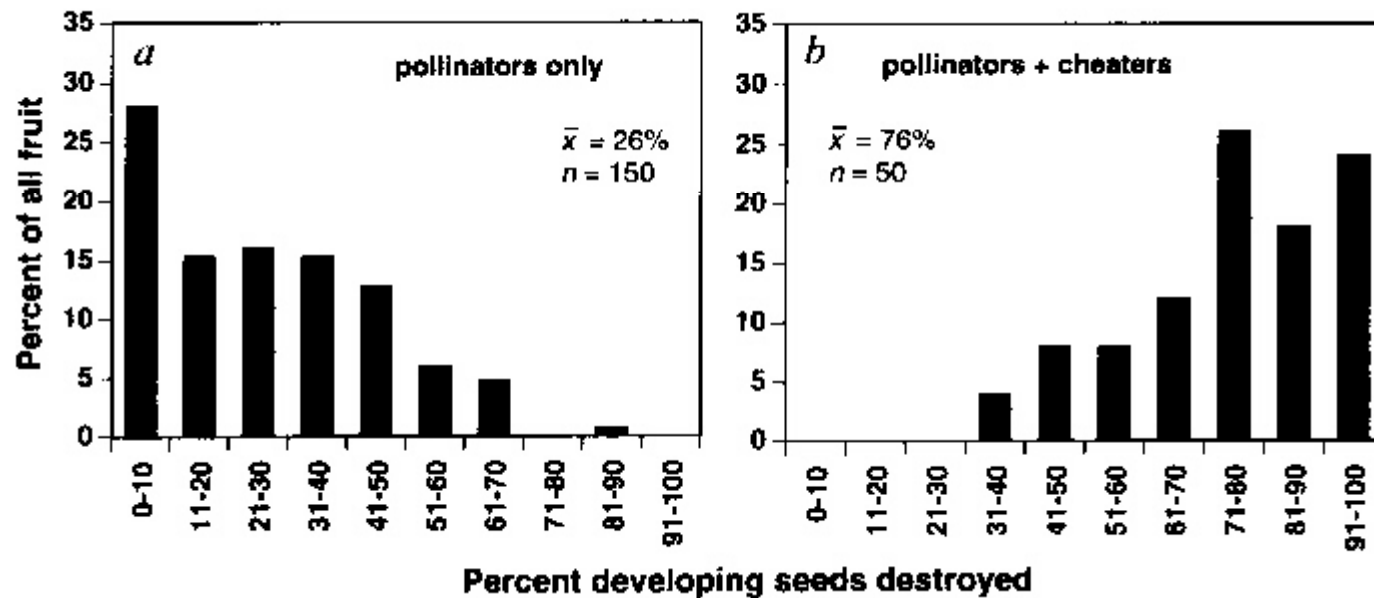
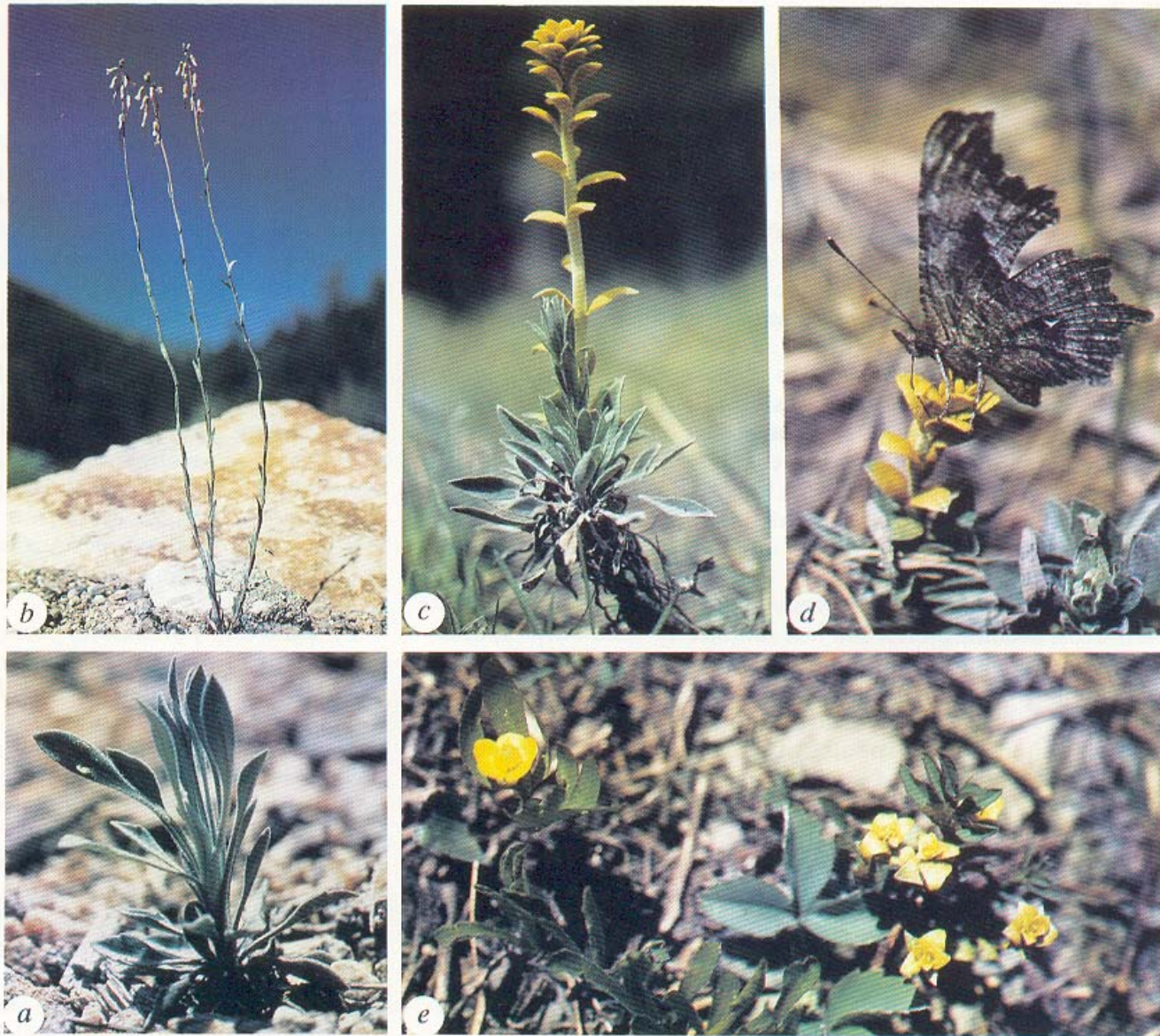


FIG. 2 Levels of seed destruction in populations of *Yucca filamentosa*, a, without and b, with cheaters. Fruits (25) were collected at random after larvae had exited from each of 8 populations in Ohio and Tennessee, and the proportion of developing seeds destroyed by yucca moth larvae was determined by seed counts.

Pellmyr, O., J. Leebens-Mack, y C.J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155-156.

FIG. 1 Morphological transformation of *Arabis* by *Puccinia monoica* rust infection. *a*, Rosette stage of uninfected *A. holboellii*. Uninfected plants remain in the rosette stage for 2–5 years. *b*, Flowering stage of uninfected *A. holboellii*. Infection of this host almost always prevents flowering and is usually lethal; in 116 pairs of infected and uninfected plants, 71% of infected plants died without flowering (versus only 12% of the uninfected plants), and none of the infected plants set seed. *c*, Bolting stage of *A. holboellii* infected by *P. monoica*. Infected plants act like they are bolting (elongation of the stem before flowering), but elongation stops long before normal flowering height is attained and true flowering almost never occurs. *d*, *Polygonia zephyrus* (Nymphalidae) feeding on the spermatial fluid of *P. monoica* on *A. holboellii*. *e*, *A. drummondii* infected by *P. monoica* (right) strongly resembles *Ranunculus inamoenus* (left), in shape, size and colour in the visible spectrum.



Roy, B.A. 1993. Floral mimicry by a plant pathogen. Nature 362: 56-58.

TABLE 2 Summary of flower sugar content and insect visitation to natural mixed plots of flowers including infected *Arabis* species

Plant species	Sugar per flower (mg)*†	Flowers in the plot (%)*	Visits to plots (%)	Time on plants (%)	Visits by flies (%)‡
Site one					
Rust pseudoflowers (on <i>A. holboellii</i>)	4.0 ± 0.70	52.0	45.1	72.2	100.0
<i>Pulsatilla patens</i>	0.12 ± 0.05	48.0	54.9	27.8	76.8
Site one total		<i>n</i> = 98	<i>n</i> = 102	108 min	<i>n</i> = 89
Site two					
Rust pseudoflowers (on <i>A. drummondii</i>)	3.0 ± 0.32	34.2	37.0	87.9	90.0
<i>Claytonia lanceolata</i>	0.06 ± 0.01	2.3	0.9	0.03	33.3
<i>Mertensia fusiformis</i>	0.17 ± 0.02	47.1	9.9§	1.3	12.5
<i>Ranunculus inamoenus</i>	0.04 ± 0.01	16.3	52.2	10.7	14.8
Site two total		<i>n</i> = 257	<i>n</i> = 324	480 min	<i>n</i> = 138

Insect observation took place between 11:00 a.m. and 3:00 p.m. during sunny, calm conditions. Site one consisted of 2.92 h of observation of three 1 m² plots near Almont in Gunnison County, Colorado (~2,700 m elevation). Site two consisted of 6.5 h of observation of three 1 by 2 m plots near Gothic, Gunnison County, Colorado (~2,957 m elevation). In all cases, insects were timed only when actually in the sexual parts of the flowers, or on the spermatial fluid of the rust fungus.

* Individual pseudoflowers were considered to be flower analogues because they are similar in shape and size to many co-occurring flowers (Fig. 1e). For example, the diameters of pseudoflowers and the diameters of flowers of *Ranunculus inamoenus* and *Claytonia lanceolata* differ only slightly: 10.67 ± 0.39 mm, versus 11.47 ± 0.21 mm and 14.87 ± 0.29 mm, respectively, *n* = 40. Sugar content data are typically reported on a per-flower basis whether the flowers occur individually or in inflorescences^{12,13}. Here, single pseudoflowers are compared with single flowers. In the list above, only *Mertensia* has flowers in inflorescences.

† Sugar in spermatial fluid is fructose (identified chromatographically using Smith's solvent²⁹ of ethyl acetate, pyridine and water, and benzidine indicator reagent). Sugar content of 14 pseudoflowers per species was estimated by removing all infected leaves, soaking in distilled water for 1 h, and measuring sugar content of solution by refractometry. Sugar content of 20 flowers per species was estimated according to ref. 12; all sugar contents are reported as mean ± standard error, in sucrose equivalents.

‡ Fly visitors to infected *Arabis* include members of the Anthomyiidae, Bombyliidae, Calliphoridae, Muscidae, Stratiomyidae, Syrphidae and Tachinidae.

§ Actual insect visits to *Mertensia* could exceed observations; the inverted tubular flowers tended to hide visitors.

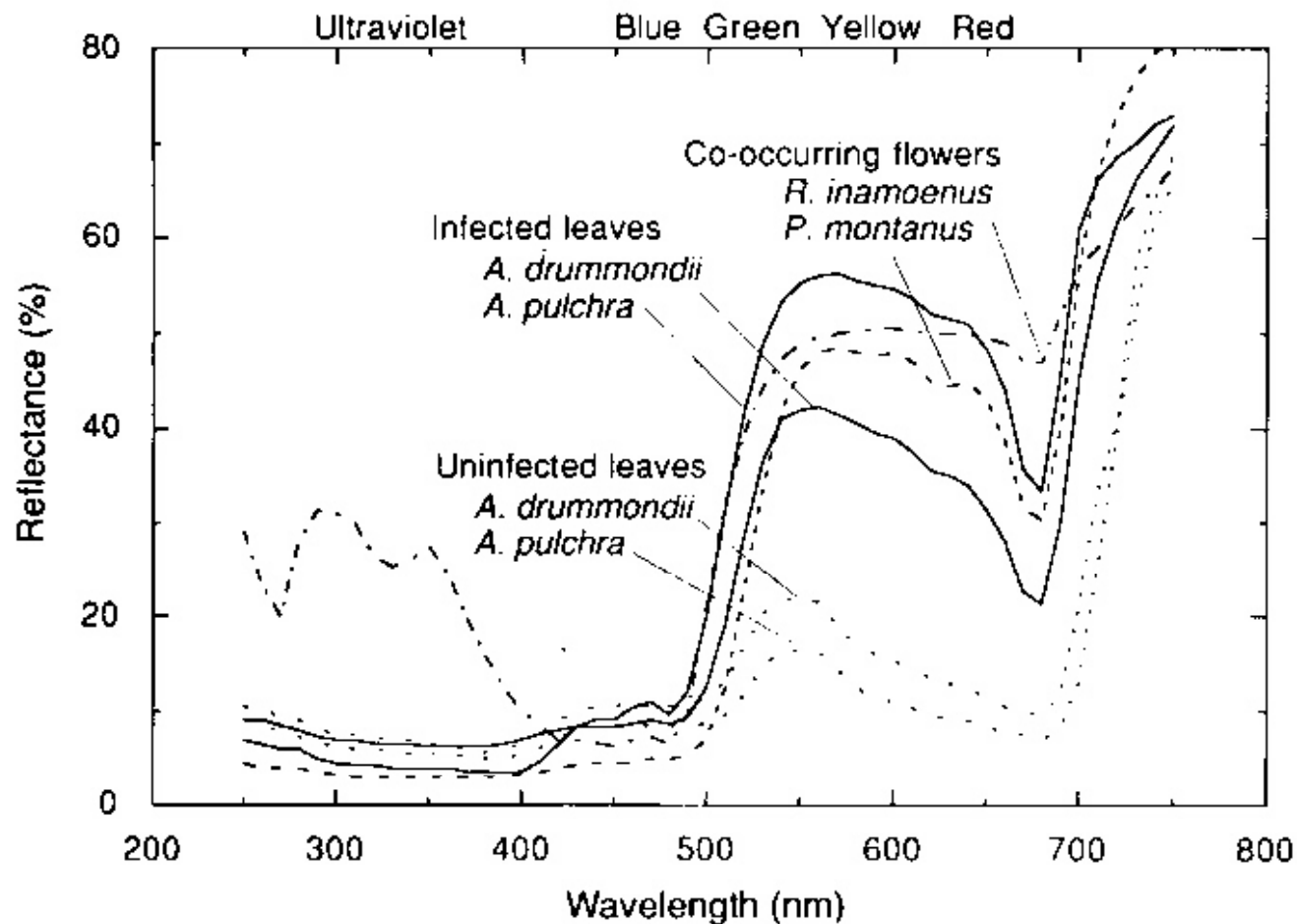


FIG. 2 Reflectance spectra of uninfected and infected *Arabis* leaves and petals of two co-occurring yellow flowers, *Ranunculus inamoenus* and *Pseudocymopterus montanus*. All spectra coincide in the visible spectrum; *Ranunculus inamoenus* also reflects in the near ultraviolet ('bee purple'). Leaves of *Arabis drummondii* were infected by *Puccinia monoica*, whereas leaves of *A. pulchra* were infected by *P. thlaspeos*. *P. thlaspeos* is very closely related to *P. monoica*³⁰ and also causes similar pseudoflowers to form on its hosts²⁴.

TABLE 1 Effect of insect visitation on rust fungus (*Puccinia monoica*) reproduction

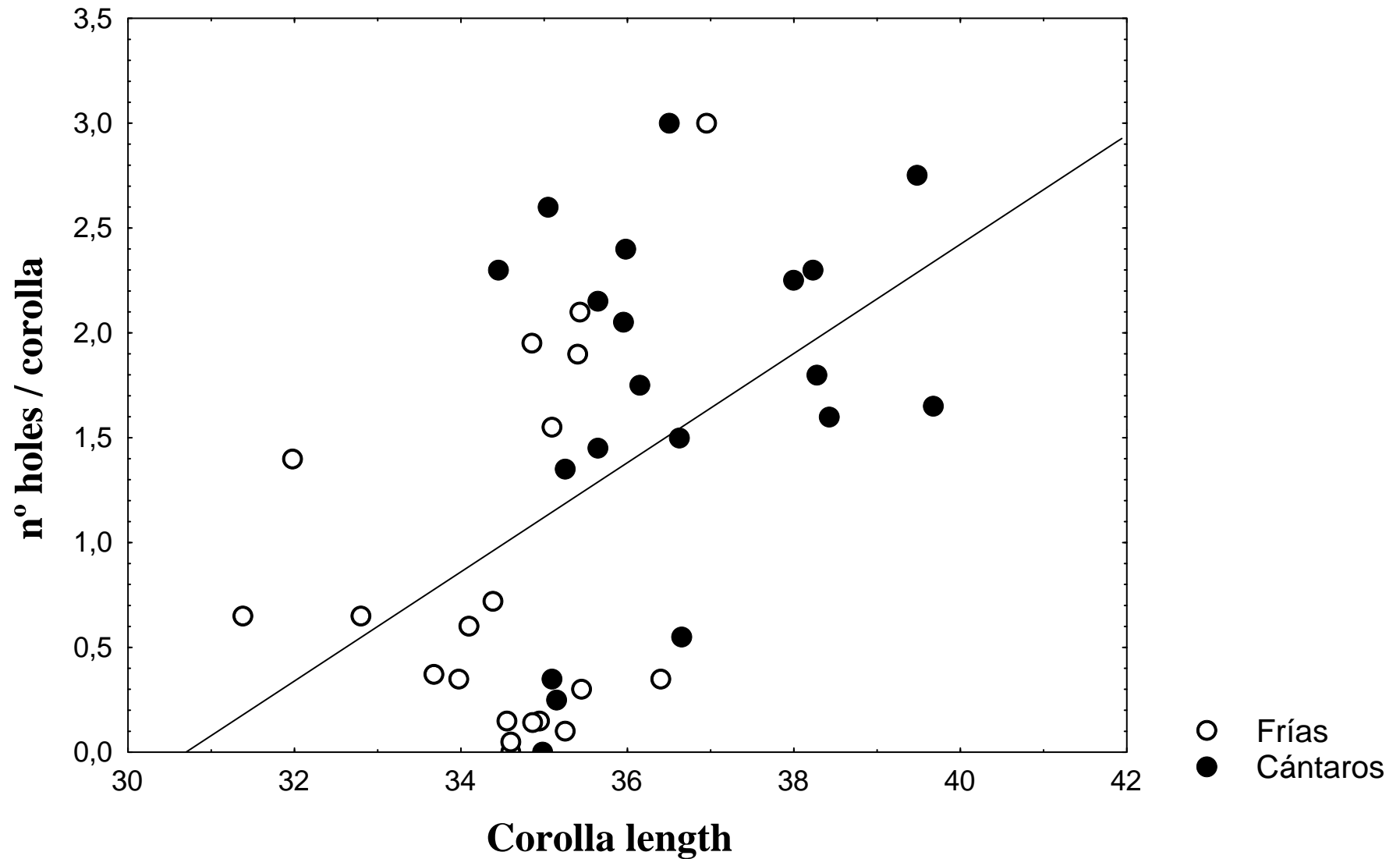
Treatment	Pseudoflowers producing aeciospores	Pseudoflowers without aeciospores	N	Likelihood ratio G*	P
Uncaged, 'open-pollinated'	20	0	20		
Caged, no pollinators	0	20	20	53.59	<0.001
Caged, 'dirty flies'	5	15	20	6.63	<0.01
Caged, 'clean flies'	3	17	20	0.05	NS
Overall test	28	52	80	63.74	<0.001

Puccinia monoica was unable to reproduce when insects were excluded. Not all infected plants that were visited by a single spore-covered fly produced spores, suggesting that: (1) the spermatia were incompatible, or (2) some caged flies did not visit the infected plant before they or the spermatia died. Some of the caged infected plants visited by 'clean' flies also produced spores suggesting that: (1) more than one mating type may be present on the same plant, or (2) the fungus is self-compatible but requires insect visitation to move spermatia between spermogonia, or (3) the putative 'clean' flies were also carrying spores. Infected plants in a meadow near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado, USA, were tagged before the fungus became sexually receptive. Tagged plants were randomly assigned to four treatments: uncaged 'open-pollinated', caged (insects excluded), caged with 'dirty flies' (caged with one spermatia-covered fly captured feeding on an infected plant), or caged with 'clean flies' (caged with one fly captured on real flowers in an area where no rust infection was found within 1 km², and therefore presumed to be spermatia-free). The flies were introduced when the rust was sexually receptive; all flies died within 4 days. Cages consisted of chicken wire cylinders surrounded by Kleen Test plant sleeves; they excluded insects while allowing light, water and wind to pass through. Uninfected plants caged in this way grew and flowered normally, indicating that the cages did not affect plant growth.

* Multiple comparisons were corrected for experiment-wide error rate of 0.05, and the likelihood ratios were corrected with the Williams correction for small sample sizes²⁸.







Urcelay, C, CL Morales y VR Chalcoff. 2006. Relationship between corolla length and floral larceny in the South American hummingbird-pollinated *Campsidium valdivianum* (Bignoniaceae). *Ann. Bot. Fenn.* 43: 205-211.

TABLE 1. Percentage of flowers robbed on plants of various species, as reported in the literature.

Robber species	Flower species	Flowers robbed (%)	Reference
Flower-piercer birds			
<i>Diglossa baritula</i>	<i>Erythrina leptorhiza</i>	91–100	Hernandez and Toledo (1979)
<i>Diglossa baritula</i>	<i>Salvia mexicana</i>	92	Arizmendi et al. (1996)
<i>Diglossa baritula</i>	<i>Fuchsia microphylla</i>	37	Arizmendi et al. (1996)
<i>Diglossa baritula</i>	<i>Penstemon kunthii</i>	50–80	Lyon and Chadek (1971)
Hummingbirds			
<i>Eupherusa exima</i>	<i>Razisea spicata</i>	98	D. Boose, <i>unpublished report</i>
Carpenter bees			
<i>Xylocopa violacea</i>	<i>Petrocoptis grandiflora</i>	44.6	Guitian et al. (1994)
Bumble bees			
<i>Bombus occidentalis</i>	<i>Corydalis caseana</i>	40–80	Maloof (2000)
<i>Bombus occidentalis</i>	<i>Ipomopsis aggregata</i>	32.9	Irwin and Brody (1999)
<i>Bombus terrestris</i>	<i>Vicia faba</i>	62	Newton and Hill (1983)
<i>Bombus terrestris</i>	<i>Corydalis cava</i>	83.9	Olesen (1996)
<i>Bombus hypocrita sapporensis</i>	<i>Corydalis ambigua</i>	71–98	Higashi et al. (1988)
Trigona bees			
<i>Trigona fulviventris</i>	<i>Lantana camara</i>	34	Barrows (1976)
Ants			
<i>Polyrachis</i> spp.	<i>Aerangis verdickii</i>	62–67	Koopowitz and Marchant (1998)
Multiple species	<i>Quassia amara</i>	83	Roubik et al. (1985)
	<i>Lonicera etrusca</i>	99	Guitian et al. (1993)
	<i>Justicia aurea</i>	81.1	Willmer and Corbet (1981)
	<i>Justicia aurea</i>	>90	McDade and Kinsman (1980)
	<i>Aphelandra golfodulcensis</i>	>90	McDade and Kinsman (1980)

Maloof, J.E. 2000. Are nectar robbers cheaters or mutualists?
Ecology 81: 2651-2661.

TABLE 2. Percentage of all flower visits to eight plant species that are from nectar robbers.

Plant species	Visits from robbers (%)	Reference
<i>Erythrina leptorhiza</i>	89	Hernandez and Toledo (1979)
<i>Quassia amara</i>	52–98	Roubik et al. (1985)
<i>Anthyllis vulneria</i>	45	Navarro (2000)
<i>Mertensia ciliata</i>	50	Geber (1982)
<i>Salvia mexicana</i>	17	Arizmendi et al. (1996)
<i>Fuchsia microphylla</i>	11	Arizmendi et al. (1996)
<i>Fuchsia magellanica</i>	80	Traveset et al. (1998)
<i>Aphelandra golfodulcensis</i>	50	McDade and Kinsman (1980)

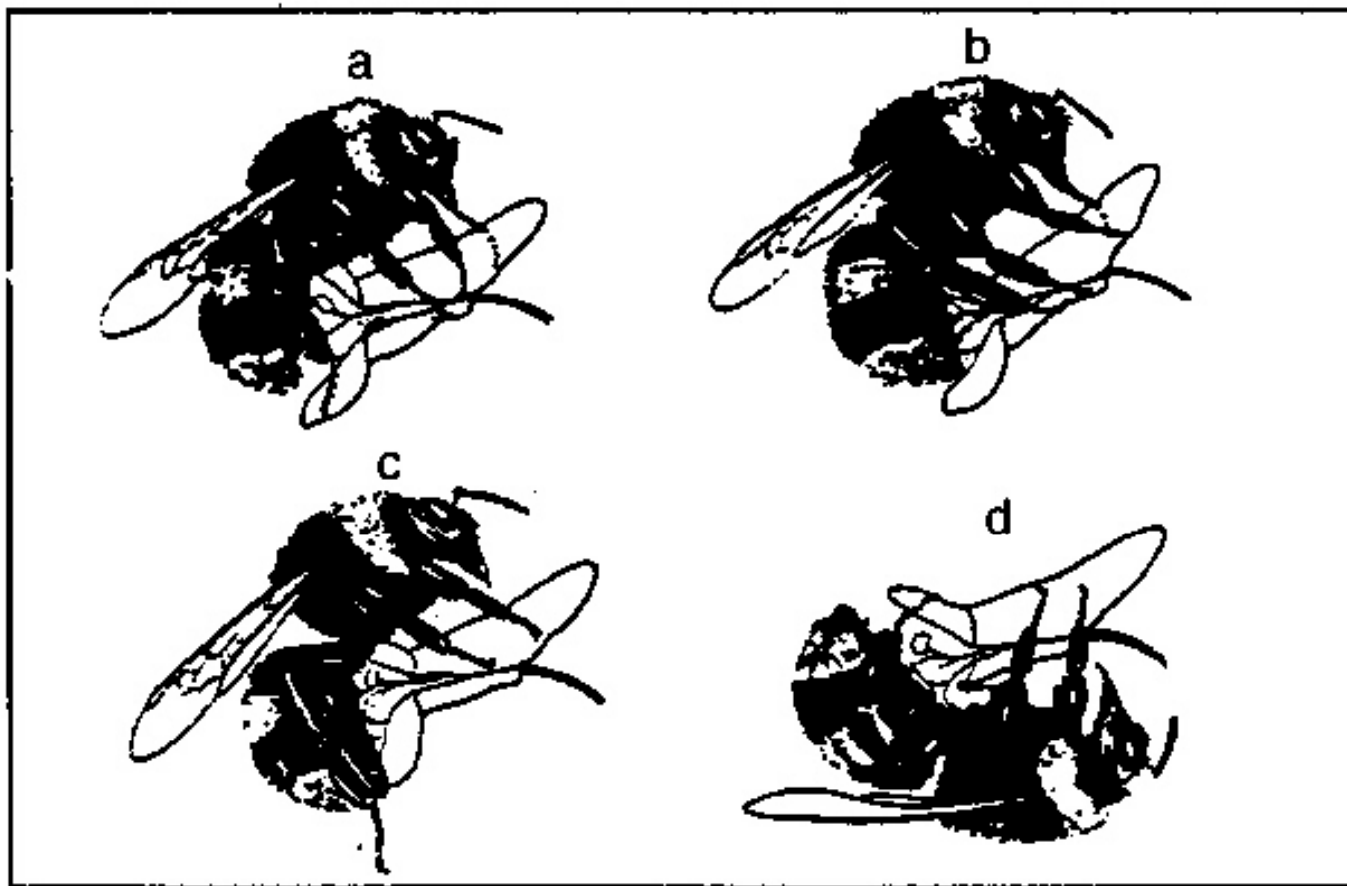


FIG. 1. *Bombus hypocrita sapporensis* on *Corydalis ambigua* flowers (from Higashi et al. 1988; used with permission from Blackwell Science Publishers). The anthers and stigma are exposed while the queens are nectar robbing (a,b) or walking around on the flower (c,d). This may result in pollination.

TABLE 3. The effect of nectar robbers on seed set of 18 plant species.

Effect on seed set	Robber(s)	Reference
Negative	birds (<i>Phrygilus</i>)	Traveset et al. (1998)
Negative	tropical bees (<i>Trigona</i>)	Roubik et al. (1985)
Negative	tropical bees (<i>Trigona</i>)	Roubik (1989)
Negative	tropical bees (<i>Trigona</i>)	Roubik (1982)
Negative	wasps (<i>Rynchium</i> and <i>Ropalidia</i>)	Reddy et al. (1992)
Negative	bumble bees (<i>Bombus</i>)	Irwin and Brody (1999)
Neutral	birds (<i>Diglossa</i>)	Arizmendi et al. (1996)
Neutral	carpenter bees (<i>Xylocopa</i>)	Guitian et al. (1993)
Neutral	bumble bees (<i>Bombus</i>)	Bilinski (1970)
Neutral	bumble bees (<i>Bombus</i>)	Newton and Hill (1983)
Neutral	bumble bees (<i>Bombus</i>)	Zimmerman and Cook (1985)
Neutral	bumble bees (<i>Bombus</i>)	Morris (1996)
Positive	carpenter bees (<i>Xylocopa</i>)	Waser (1979)
Positive	carpenter bees (<i>Xylocopa</i>)	Guitian et al. (1994)
Positive	bumble bees (<i>Bombus</i>)	Hawkins (1961)
Positive	bumble bees (<i>Bombus</i>)	Koeman-Kwak (1973)
Positive	bumble bees (<i>Bombus</i>)	Higashi et al. (1988)
Positive	bumble bees (<i>Bombus</i>)	Navarro (2000)

TABLE 4. Potential behavioral changes in pollinators caused by nectar reduction by nectar robbers. The probable result for the plant assumes that all other behaviors remain the same on robbed and unrobbed flowers.

Behavioral changes in pollinators	Probable result for plant
Flight distances increase	Pollen flow distance increases
Fewer flowers visited on each inflorescence	Reduces geitonogamy in self-fertile flowers
Visit more flowers per unit time	Pollen flow rate increases
Reduced time spent in each flower	Less pollen transfer
Change foraging tactic to pollen collection only	Depends upon the morpho- logy of the plant
Avoidance of robbed flowers	Could increase pollen flow distance if pollinator does not switch to different species
Switching to a different plant species	No pollen transfer